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THE CONCEPTION OF SPECIES AS AFFECTED BY RECENT INVESTIGATIONS ON FUNGI.¹

W. G. FARLOW.

THE fiftieth anniversary of the foundation of the American Association is a fitting occasion for a retrospective view of the different branches of science represented in our Society, and one would be glad to hear, from the lips of some botanist who was present at the first meeting of the Association, an account of the changes which have been brought about in the methods of botanical study and research, and of the progress which has been made in North America during the past half-century. Fifty years, however, is a long time in the life of any individual, and of those who in 1848 were young, or comparatively young, even the most favored could hardly be expected to retain their scientific activity in 1898. On glancing over the list of members in 1848, one sees the familiar names of a number of botanists, including Ashmead, J. W. Bailey, Barratt, Jacob Bigelow, Buckley, Dewey, Emerson, Engelmann, L. R. Gibbes, Gray, B. D. Greene, Edward Hitchcock, Oakes, Olney, Pickering, Thurber, Torrey, and Tuckerman. Not one of these leaders of American botany in their day remains to tell us of the Association in its infancy and to trace its development with the vividness which personal experience alone can supply.

It would be scarcely fitting in me to attempt to give a general sketch of the part which botany and botanists have played in the life of the Association; nor, remembering the review of recent investigations in botany presented by Prof. Marshall Ward at the meeting in Toronto last year, is it desirable that I should encroach on the ground so thoroughly and so interestingly covered by him. I may, however, on this occasion, be permitted to say a few words on a single question on which opinions have changed very much during the last fifty years,

¹ Address of the Vice-President and Chairman of Section G, Botany, at the fiftieth anniversary meeting of the American Association for the Advancement of Science, Boston, August, 1898.

and, avoiding a detailed history of the subject, treat it somewhat abstractly in its general bearings ; for the question, you will admit, is one about which we should occasionally ask ourselves what is probably or possibly true, without, however, expecting, in most respects, to be able to reach positive conclusions. What do we mean by species? Do species really exist in nature, or are they created by us for our own convenience? As I do not pretend to be in the position of a philosopher, but approach the subject as a very commonplace sort of a botanist, the word species, as used by me, means simply species as understood by the systematic botanist, and indirectly by those working in other departments of botany who are obliged to depend to a considerable extent upon the limitations of species as defined by systematists.

The publication of the *Origin of Species* in 1859, a date which marks the fall of the old school and the rise of the new, is sufficient to show that it is not probable that any other period of fifty years in the future will have the same comparative historical importance, as far as the question of the conception of species is concerned, as the fifty years we are now commemorating. Had we asked any of the botanical members of the Association in 1848 what they meant by species, they would have replied, most of them without reserve, a few with some hesitation, that in the beginning God created all species as he intended them to be, and that, by searching, the naturalist could find them out. Just how they recognized species when they saw them would have been very hard for them to say, as they did not agree in their standards; but they would probably all have agreed in saying that the recognition of species was a matter of individual judgment, one's own judgment, of course, being better than that of any one else. The sceptic at that time could not have failed to notice the frequency with which what was home-made was confused with what was God-given. Before 1859 creation was one vast pudding, in which the species had been placed like plums by an Almighty hand, and the naturalists, sitting in a corner like greedy little Jack Horners, put in their thumbs and pulled out the plums and cried, "See what a great naturalist am I — I have found a new species!"

Probably very few of my hearers have any personal recollection of the time when not to believe that species were fixed and immutable creations was enough to make one a scientific and almost a social outcast. I recall but a few people whom I knew who held these orthodox views, for it was my good fortune to be a student in college at the time of the appearance of what was called "a new edition of the *Origin of Species*, revised and augmented by the author," published by D. Appleton & Co. in 1864. By that time the novelty and audacity of Darwin's views had ceased to cause a cold shudder, and certainly the students of my time were ready to swallow not only what Darwin had written, but to add a few little theories of their own.

The young botanist of to-day will, I think, pardon me, although my contemporaries may not, if I give a short sketch of the Harvard Natural History Society in the sixties, as showing not only how changed is the position of Natural History in American colleges, but also the attitude of college students at that day toward the then new doctrine of evolution. If the Society soon after my college days passed out of existence, its end could not be said to be untimely, for the attitude not only of the university but of the scientific public towards the study of natural history had so changed that the old-fashioned Society had no place. Those of you who go to Cambridge next Friday may perhaps see a dreary, barn-like sort of a lecture-room which now occupies the greater part of old Massachusetts Hall. In days gone by the three upper stories of the hall served as dormitories, and the lower story was occupied by the rooms of the Natural History Society, sandwiched in between those of the Institute of 1770, which then was pleased to consider itself to be a literary society, and the laboratory of the Rumford Chemical Society, which, as it emitted none of the odors characteristic of chemical activity, must be considered in my day to have been moribund, if not actually defunct.

The rooms of the Natural History Society would now cause a smile. From the low ceiling were suspended an alligator, a turkey buzzard, and such other creatures as would not fit well in the wall cases. In one corner leaned lazily a large cup sponge, a receptacle for the dust which gravity constantly supplied and

the rejecta contributed at frequent intervals by the members. Around the walls was a very promiscuous collection of birds and mammals, some shot and prepared by past members, others the gift of so-called benefactors, who, not knowing what else to do with them, turned them over to the Society. Quartz crystals and other showy but not very valuable minerals hobnobbed with skeletons, one of which, at least, must have been very useful, if one could judge by the perennial absence of some of the limbs, which had been removed, as was said, for study.

Botany was represented by a single cabinet, whose pigeonholes were filled with plants of New England, enriched by choice fragments of specimens collected by well-meaning persons in the Alps and by travelers in the Holy Land. The plants were arranged, or rather shuffled, in the case according to the wishes or necessity of the curator of the time being. We were quite eclectic in our view of botanical classification, some pigeonholes being arranged on the Linnæan system, some on the natural system, and some apparently alphabetically. Whatever real value the collections may have had, once a year they were at least ornamental. Every year the members were photographed, and the alligator, the turkey buzzard, and the human skeleton were taken down and added to the group to show that we were really the Natural History Society, and not the Hasty Pudding or the Phi Beta Kappa.

The old collections were long ago dispersed, and the little which was of value is now incorporated with the different university collections. You may perhaps be curious to know what the members of the Society did. That is easily told. They all talked, and some dissected cats. The talk was to a great extent about the origin of species, and, no matter what was the subject of the papers announced for the evening meeting, it was not often that we adjourned without dropping into a discussion of evolution. Few had really read Darwin's book, but all felt able to discuss the great scientific question of the day, in which respects, perhaps, we did not differ from some older and more learned people. Although the traditional man who is always on principle "on the other side" was not wanting, we were practically unanimous in our opinion. We all

felt that a new day had dawned; that the old view of looking at species as fixed creations, and ignoring as far as possible the significance of their tendency to vary, had been forever upset by Darwin, and that hereafter we must look to evolution as brought about by natural selection to interpret species as we now find them. Not being well informed in regard to the history of scientific opinion, we assumed somewhat hastily that before Darwin all was darkness, and we did not trouble ourselves to go back and inquire whether there were not others who had had at least glimpses of the great truths of evolution; but even had we heard that there were some before Darwin who did not believe in the fixity of species, it would still have been true that it was Darwin's book by which, practically, the world at large was enlightened on the subject.

Forty years have passed, and inasmuch as we are all evolutionists, either of the Darwin school or some related school, the question suggests itself, Is our belief in evolution merely dogmatic, like some of the theological doctrines which we believe thoroughly but which we do not allow to interfere with our daily life, or, as far as botany is concerned, has our belief modified the manner in which we treat what we call species? The mere fact that we now recognize that species have been derived from other species, and are on the way to develop into still other species, would naturally lead us to be more liberal in our treatment of them systematically than in the days when variation was almost a crime against the Almighty. Certainly, with evolution as a key to guide us, our conceptions of genera and orders ought to be far more scientific than they were.

A species has been defined as a perennial succession of like individuals; and, although no definition is perfect, I doubt whether a better definition of species has ever been invented. It is a peculiarity of definitions, however, that they all need to be defined. In the present case we must be told what is meant by the word perennial, and what is meant by like. To the pre-Darwinian, perennial, of course, meant for all time. By the early Darwinians we are not told whether by perennial they meant a hundred, a thousand, or a million years; but until at least we know approximately what is meant, we must still ask

how long must be the succession of like individuals to establish a good species. Otherwise the whole matter of the distinction between a race and a species cannot be settled practically. If there is nothing definite in writings of the time of Darwin to explain the limits of the perennial succession, we should bear in mind that the object then was to bring out boldly the salient points of evolution as governed by natural selection, and the illustrations used were taken almost exclusively from the higher animals and plants in which the lives of individuals are of such duration that it was impossible to obtain accurately the records of a large number of generations in any case. Enough was shown and cited to show from the records of comparatively few generations a general tendency, which it was assumed would be confirmed could the geological record be followed, and we can suppose that, so far as they considered the question at all, the early Darwinians took it for granted that the perennial succession needed to establish a species covered very long intervals of time. While one need not object to this method of reasoning, it is plain that the practical question of when a race or variety ceases to be a race and becomes a species was left open, and it is questions of this sort which the systematist is constantly called upon to answer.

What could be learned only slowly and fragmentarily from observations and experiments on higher plants and animals might perhaps be learned much more easily could one experiment with organisms whose cycle of life is completed with great rapidity. For this purpose one might suppose that nothing could be better than bacteria, which are easily managed in the laboratory, and whose development takes place with such rapidity that it is possible for the experimenter to watch the course of hundreds or even of a thousand generations in a comparatively short time.

The advantage to be expected from studying forms in which the development is very rapid is, however, made difficult for purposes of comparison by their extreme simplicity and the difficulty, and at times impossibility, of finding sufficiently marked morphological characters to guide us; and in the absence of such characters the bacteriologist is often forced to base what

he calls his species on physiological characters, including in that term zymotic and pathological action. By botanists, who are not specially bacteriologists, the so-called species of bacteria are not admitted to be species in the proper sense. Whether scientifically considered they are not as legitimately species as what are called species in speaking of the higher plants, is a very pertinent question. Any definition of species, to be scientifically accurate, must in its essential points apply to all plants and all animals; and if a species of flowering plant is a perennial succession of like individuals, it is hard to see why in bacteria a perennial succession of like individuals does not also constitute a species. That the individuals in bacteria are very different from the individuals in flowering plants is certainly true, but that does not affect the question of the validity of the species in the former. As far as the perpetuation of morphological likeness of the individuals is concerned, there is no doubt that it is, to say the least, as complete in bacteria as in flowering plants, and the physiological constancy has been shown by competent observers to persist in some cases for hundreds of generations. That these many generations have been produced in months rather than in hundreds of years does not, it seems to me, affect the case.

When, therefore, the botanist denies that physiological species are properly species, he is practically admitting that his own definition, the perennial succession of like individuals, is used by him in a special sense, and he does not seem to be aware that species as he limits them are artificial and not natural. The belief that species should be based on morphological rather than physiological characters rests on the assumption that the former are more likely to be inherited, and thus show the ancestry, while the latter are more likely to be the result of the temporary attempts of the organism to adapt itself to the environment. It is perhaps a question whether the grounds for this belief are as valid as has been supposed. We readily see morphological characters which have been inherited, but it is usually only by accident or experiment that we recognize the physiological or pathological qualities.

Let us turn for a moment from bacteria to *Saccharomycetes*,

whose characteristic function is to invert and ferment the different sugars. Here we have a group much more limited in number of species than the bacteria, but like them microscopic and rapidly growing. Although not long ago they were classified after a fashion on their morphological characters, the admirable investigations of E. C. Hansen and his followers have pointed out the important fact that these characters, taken by themselves, are less fixed, although the limits of their variation may be fixed, than certain physiological characters such as the maximum and minimum temperatures of growth, and especially the temperature at which spore formation takes place. It is in these last-named characters, rather than in the former, that the specific distinctions in *Saccharomycetes* are sought by those who study that group specially.

The same objection is urged by botanists in this as in the case of bacteria, that the so-called species are not species, but races. We naturally ask, races of what species? There have been many attempts to determine the origin of the common *Saccharomycetes*, and the question has been supposed more than once to be settled. Without intending to imply that the question is not still open to investigation, I must admit that there does not yet seem to me to be any satisfactory proof to show from what higher forms *Saccharomycetes* have been derived. Although there can be no doubt that in the germination of spores of certain fungi, especially the *Ustilaginaceæ*, bodies are produced in abundance which not only closely resemble *Saccharomycetes* in shape, but also, in some cases at least, are capable of producing alcoholic fermentation to a limited extent, it does not seem to me that that is by any means enough to warrant the opinion expressed by Brefeld that the *Saccharomycetes* are derived from, and are degenerate conditions of, *Ustilaginaceæ*. In fact, one has only to consult Brefeld's own writings to see that *Saccharomycetes*-like bodies are produced by the germinating spores of other orders of fungi than *Ustilaginaceæ*, and it is known that, in some species, as in the genus *Aspergillus* and in certain *Mucoraceæ*, the budding cells which look like the *Saccharomycetes*, using the word in the limited sense, are also capable of producing alcoholic fermentation.

On the other hand, no one has yet succeeded beyond a doubt in making the *Saccharomycetes* proper revert to a higher ancestral form. I say beyond a doubt, because the observations of Juhler, Joergensen, and Johan-Olsen, on the relation of *Aspergillus*, *Sterigmatocystis*, and *Dematium*, to *Saccharomycetes*, have not been confirmed by other equally good observers, as Kloecker and Schioenning; and, for the present at least, we must regard the observations of Joergensen and Johan-Olsen as affording still other instances of the fact that under proper conditions the germinating spores of many fungi produce bodies like *Saccharomycetes*, while they do not show conclusively that forms recognized by specialists as genuine *Saccharomycetes* can be transformed into fungi of other orders. They do, however, show that the views of Brefeld that the *Saccharomycetes* are derived from *Ustilaginaceæ* could, at the best, be only partially true.

Let us return to the question as to whether or not species of the *Saccharomycetes*, as defined by Hansen for instance, should be allowed to be called species in the proper sense of the word. Of course no one supposes that they have always existed in their present form, and, although we have no exact knowledge of the ancestors of the present species, we naturally suppose that they were derived from some other higher fungi, as the expression goes. Whether derived from one particular order of fungi or from several different orders, the species as we now see them seem to be constant in the sense that that word must be used in speaking of species of any group of plants. The shape of the cells in any given species, although variable to some extent, is constant within definable limits, and, although they have periods of rest and periods of activity, their physiological action seems to be the same under similar conditions.

We might be justified, it seems to me, in regarding as races the *Saccharomycetes*-like forms which result from the germination of spores of higher fungi, provided they continued to live an independent existence for a time and were not, as is more likely to be the case, merely accidental conditions depending on unusual or unfavorable conditions of germination, but the *Saccharomycetes* in the limited sense are constant, as far as

constancy is to be expected in living organisms in general; they cannot be made to revert. as far as we know, and I therefore fail to see why they should not be admitted to be scientific species. The same is true of the physiological species of bacteria, meaning, of course, those which have been well studied, and excluding the mass of ill-described and ill-known forms which abound in bacteriological writings. When a race has become so constant that it no longer reverts, and we cannot tell from what species it came, it is no longer a race, but a species.

It may be objected, however, that both bacteria and Saccharomycetes differ from ordinary plants in a most important respect, *viz.*, that there is a complete absence of sexuality and the reproduction is purely vegetative. There are a few botanists, to be sure, who think that there is a form of sexuality in Saccharomycetes, but botanical opinion at present is so overwhelmingly on the other side that to call the question an open one would require an explanation which time will not permit. It may be urged that in plants in which sexuality is wanting we have no right to speak of a perennial succession of like individuals, for, it may be claimed, succession means by sexual generation only. This interpretation is very convenient if one wishes to ignore forms like bacteria and Saccharomycetes in the consideration of the question of species, but to exclude them on this ground is somewhat dangerous unless we are prepared to admit, offhand, that species are purely artificial.

It is the custom to speak of bacteria and Saccharomycetes as degenerate forms. What is meant by this expression is not plain, unless it means that, arising presumably from plants in which sexuality was present, they have become non-sexual. Undoubtedly sexuality is the rule in nature, but it should be borne in mind that it is not universal. I do not refer here to fungi like Ascomycetes and Basidiomycetes, which, accepting the hasty conclusions of the Brefeld school, have been, even by a good many of our own botanists, included in the limbo of non-sexual degenerate forms, from which more recent observers are gradually rescuing them. I refer rather to species like *Rhodymenia palmata*, one of the commonest red seaweeds of the North Atlantic, in which, so far, nothing has been discov-

ered but the non-sexual tetrasporic reproduction. This is not an isolated case, and others will probably occur to my hearers. Furthermore, we must admit that the number of species normally sexual, but in which apogamy sometimes occurs, has been perceptibly increased by the studies of botanists in recent years. In such cases as that of *Rhodymenia* it may be that the cystocarpic fruit really exists, and will be found later, but, since botanists have searched for it in vain for many years, it must be very rare, and certainly, as far as we know it, the plant is non-sexual.

In regard to cases of apogamy, we have not yet sufficient data as to their capacity for propagating themselves continually apogamously, although in such cases as that of *Chara crinita*, if we may judge by the distribution of the species in central Europe, there seems to be no reason to believe that they may not do so indefinitely. The not inconsiderable number of species of mosses, some of them common species, in which the male or female only is known, and the number of marine algæ, which, in spite of their frequency, bear only tetraspores, or at most bear cystocarps very rarely, should make us cautious in so defining what we mean by species as to imply that we consider that the perennial succession refers only to succession by sexual generation.

We cannot fail to notice an increasing tendency among cryptogamic botanists to give more and more weight to physiological characters in limiting their species. For some time we have been accustomed to think of the species of bacteria as largely physiological, and we are gradually accustoming ourselves to the views of those who hold the same view in regard to species of *Saccharomycetes*. More recently still we find that in another higher order of fungi, the *Uredinaceæ*, experts are coming more and more to rely on physiological characters. If in bacteria and *Saccharomycetes* we have plants which are generally recognized to be non-sexual, in *Uredinaceæ* the probability is that there is sexuality; at least, the probability is here much stronger than in the other two groups. By some the sexuality of *Uredinaceæ* is considered already proved, but admitting that the form of nuclear union demonstrated by Dangeard and Sappin-Trouffy, and confirmed by some other botanists, must have some impor-

tant significance, not only in this but in other orders of fungi where it occurs, there are reasons for not regarding the union in this case as representing true sexuality. On the other hand, although no one has as yet quite proved it, there appear to be reasons for supposing that, in the æcidial stage, a form of true sexuality occurs, comparable with what is known in some ascomycetous fungi. Time alone will show whether this present probability is a reality, but at any rate the position of Uredinaceæ in regard to sexuality is undoubtedly very different from that of bacteria and Saccharomycetes.

One who takes up the recent descriptive works on Uredinaceæ is surprised to see the number of species which depend on physiological characters. The former method of describing the species of this order from the morphological characters of the teleutosporic, the uredosporic, and æcidial stages, was certainly sufficiently perplexing, but one almost gives up in despair on seeing species in which the different stages are identical in all respects, except that some of them, usually the æcidia, will grow only on certain hosts. Facts like this are of course only determined by artificial inoculations, although they may sometimes be suspected by the distribution of the different stages in nature. In this complicated state of things, more complicated than in any other order of plants, we are compelled to examine very critically the accounts of cultures made even by botanists of high reputation, and it is only natural that we should hesitate to give implicit confidence to negative results unless the observations have been repeated by other observers at other times and places. Even from scattered positive results one should avoid drawing too wide general conclusions. We may readily believe that some of the supposed distinctions in the choice of their hosts by different Uredinaceæ will be proved hereafter not to be founded in fact, but, making all proper allowances for possible errors in observations and for hasty speculation in a field where speculation is so easy, and accurate experiment so difficult, we have to admit that in a good many cases surprising results have been confirmed by repeated observations, and the tendency to split up species on physiological grounds becomes more and more marked.

As the subject is somewhat complicated, it will be well to consider a few prominent cases by way of illustration. An instructive case is that of the Puccinia on *Phalaris arundinacea*, referred to, among other subjects, by Magnus and Klebahn in papers published in 1894 and 1895. To the teleutospores was originally given the name *Puccinia sessilis* Schneider, which was found by Winter to bear its æcidia on *Allium ursinum*. Later Plowright experimented with a species which grew on *Phalaris* whose teleutospores could not be distinguished from those of *P. sessilis*, but whose æcidia could be produced on *Arum maculatum*, though not on *Allium*. To this physiological species Plowright gave the name of *P. phalaridis*. Still later Soppit discovered that a Puccinia indistinguishable from *P. sessilis* and *P. phalaridis* in its teleutospores produced its æcidia on *Convallaria majalis*. To this species he gave the name of *P. digraphidis*. Had these observations not been confirmed by others we might have doubted whether Winter, Plowright, and Soppit had not really experimented with the same species of Puccinia, but, owing to some accident of their cultures, had succeeded in inoculating only different hosts, whereas it might well be the case that the æcidia on the three hosts might by subsequent cultures prove to be the same; and, in that case, *P. sessilis* would really be only an instance of a Puccinia which produces æcidia on three different hosts, not an infrequent case. The observations of Magnus showed that *P. digraphidis* bore æcidia also on *Polygonatum* and *Maianthemum*, genera closely related to *Convallaria*. So far as concerned *Polygonatum* and *Maianthemum*, Soppit and Magnus's observations were confirmed by Klebahn. The case is complicated by a difference of opinion as to whether the æcidium on Paris is connected with *P. digraphidis*, or whether there is not a fourth distinct species, *P. paridis*, as believed by Plowright.

We need not stop to consider the further history of this complicated case, as it is introduced here merely to illustrate the method and tendency of recent workers in this field.¹ The above-named botanists, who studied the species of Puccinia on

¹ Those interested in the subject should consult Klebahn, "Ueber den gegenwärtigen Stand der Biologie der Rostpilze," in *Botanische Zeitung*, May 16, 1898.

Phalaris, seem to agree in speaking of *P. sessilis*, *P. digraphidis*, and *P. phalaridis* as distinct species, although Plowright considered *P. paridis* to be distinct from *P. digraphidis*, whereas Magnus considered the two to be what he calls adaptive races (Gewohnheitsracen) of the same species. Magnus speaks of the three species as biological species, which he distinguishes from adaptive races, the latter including forms in which, although the æcidium may be produced on different hosts, it does not appear to be so frequent or so well developed on some hosts as on others, showing in the one case that the adaptation is more complete than in the other. Klebahn, although admitting that it is not of real importance whether one regards such forms as the Pucciniæ on Phalaris as species or races, nevertheless states that he sees no reason why they should not be considered to be genuine species rather than races.

Another instance in point is the group of æcidia generally known as species of *Peridermium*, which infest species of *Pinus*. It had for some years been recognized that the æcidial stage of the corticolous form of *Peridermium pini* was not the same as that of the form on the leaves, but in recent years the subdivision has been carried much farther, owing to cultures made by Klebahn, Edouard Fischer, Rostrup, and others. The former has distinguished at least seven species of *Peridermium* on *Pinus sylvestris* alone, whose uredo and teleutospores are to be found in the species of *Coleosporium*, which grow upon different genera of Compositæ, Scrophulariaceæ, and Campanulaceæ. Although Klebahn is inclined to see minor differences in the shape and markings of the æcidial spores of some of the species, it must be admitted that the differences in some cases are so slight, both in the case of the æcidial spores and the corresponding teleutospores, that, were it not that cultures show the connection between the form on one host with that on another to the exclusion of other hosts, it is hardly likely that many botanists would consider them as distinct species.

The most suggestive Uredinaceæ for our present purpose are the different species of *Puccinia* which attack grains and other grasses, for a knowledge of which we are indebted to the

researches of Eriksson and Henning in Sweden, whose work is certainly a model of careful investigation. I take it for granted that most of my hearers are already acquainted with the character of the work in question, and we need stop to consider only those points which bear upon the subjects we are discussing. Of the three common rusts which affect grains, *Puccinia graminis*, *P. rubigo-vera*, and *P. coronata*, the æcidia are to be found, respectively, in *Æcidium berberidis*, *Æc. asperifolii*, and *Æc. rhamni*, according to the previously accepted view in regard to those species. Judging by the morphological characters of the teleutospores and the uredospores alone, these three species occur on a large number of different grasses. In making inoculations to ascertain the facts in regard to the æcidia of the species, Eriksson and Henning found that what was supposed to be *P. graminis* growing on *Phleum pratense* and *Festuca elatior* had no æcidia, and they described this form under the name of *P. phlei-pratensis*. *Puccinia coronata* is separated into two species, *P. coronifera* and *P. coronata*, the former having its æcidium on *Rhamnus catharticus*, the latter with æcidia on *Rhamnus frangula*, with perhaps two other forms to be separated from the old *P. coronata*. *Puccinia rubigo-vera* is separated into three species: *P. glumarum*, *P. dispersa*, and *P. simplex*—the distinctions based largely on the presence or absence of the æcidium, although there are also certain differences in the habit and color of the other stages. The three original species are split up into seven species, besides two uncertain forms, characterized in the main by physiological characters. Furthermore, of *P. graminis*, six specialized forms are enumerated, characterized by differences in the inoculating capacity of the uredo or teleutospores on different hosts. The other species also have their specialized forms, the total number being, I believe, twenty-eight. We may consider the specialized forms to be races, and, in that case certainly, we shall have to agree with Eriksson and Henning in considering their seven species as species rather than races. The important point is to know whether the differences observed are temporary and accidental or permanent. It is too much to ask for the confirmation of the results of these two experimenters just

now, for their work is recent and has been carried so far beyond that of previous experimenters that it must require a considerable number of years before we can expect the work to be repeated by others. So far as the experiments have been repeated, as in the case of *P. coronifera* and *P. coronata*, it has been confirmed.

Enough has been said to show that the conception of species by those who are doing the most advanced work in fungi is much more flexible than it used to be, and significance is to be attached to the fact that the number of those who, as viewed by the typical systematic botanist, hold very heterodox views is increasing. The explanation is to be sought in the fact that descriptive botany in certain groups of plants has reached a point where the ordinary morphological characters no longer suffice to classify what we know or wish to know about the plants themselves. It was my privilege eleven years ago to address what was then the biological section of the Association on a subject somewhat related to that of to-day, and my closing sentence then was: "Following the prevailing tendency in business affairs, the question they [botanists] ask of plants is not so much, 'Who is your father and where did you come from?' as, 'What can you do?'"

The tendency noticed eleven years ago is even more marked at the present day. As compared with the times of which I attempted to give a sketch in my opening remarks, I think we may truly say that whatever may be the case in zoology, in botany theoretical considerations with regard to evolution play a much less important part than they used to. In the case of such plants as Lycopodiaceæ, Equisetaceæ, and their allies, and of certain orders of phanerogams, the ancestral question naturally remains as important as ever; but, although papers on other orders of plants, accompanied by hypothetical genealogies and family trees of the banyan type, appear at not infrequent intervals in botanical journals, they are quite overshadowed in general interest by the papers on cytology, life histories, and physiology. That was not the case in the sixties, when nothing compared in interest with the question of the origin of species. While we cannot be too grateful to Darwin for having opened

our eyes to see the value of evolution in general, the majority of the active botanists of the present day find too many other pressing questions to be solved to be able to dwell on evolution to the same exclusive extent as did the botanists of the last generation.

Our definition of a species included two terms which required further explanation. We started out in the hope of finding some light as to the approximate length, or at least the approximate minimum of the length of time which is needed to transform a race into a species, hoping that perhaps those plants in which the development of the individual was rapid might show that in a comparatively short space of time a race might be actually observed to become fixed and be considered a species; a fact which certainly could not be so well ascertained by direct observation in the study of the higher plants alone. You will notice that, like the obliging shopkeeper, I have not given you exactly what you expected, but have offered you instead something else perhaps just as good, if not better. If I have not been able to tell you that in such simple and quickly growing plants as bacteria and *Saccharomycetes* new species can be produced from old ones in a comparatively short time, a consideration of some of the peculiarities of such plants has brought out the modifications which have taken place in the views of a good many as to specific limitations, which is in part an answer to our primary question, What do we mean by a species?

It may be added that although some of the species of lower plants may be transformed in various ways by artificial cultures, on the whole we are quite as much struck by their comparative constancy in important respects as by their tendency to differentiate. In *Uredinaceæ* there is a tendency to form adaptive races, which is greater than was formerly supposed; but whether the tendency is greater than would be found in some higher plants, were they studied as carefully as have been the *Uredinaceæ*, is perhaps a question. Parasites, as a rule, are more plastic and more sensitive to changes of environment than other plants, and their impressionability, if I may use that word, might be expected to accentuate their power of specific transformation. It cannot be denied that there is a general suspicion, to say knowl-

edge would be too strong, that the lower plants become specifically changed more easily and quickly than the higher; but although this is what we should expect from their more rapid individual growth, I am not able to cite any actual observations which can settle the question; for, as you know, the school of botanists, which may be called the school of ready transformationists, have a fatal tendency to accept unskillfully conducted or otherwise faulty observations as convincing proofs. Others, it is to be feared, err on the other side, and are not sufficiently ready to admit metamorphoses in different species of the lower plants. Probably the truth lies between the two. The metamorphoses to which I now refer are, of course, in the normal cycle of individual development and should not be confused with the differentiation into races and species, but of necessity our views as to the latter must be influenced to some extent by our attitude towards the former.

If we turn to the second word of our definition which needed explanation, and attempt to say what is meant by like individuals, we find ourselves wholly at sea. Even if we agree that the likeness must be morphological and not physiological, that does not help the matter at all. No two individuals are ever absolutely alike in morphological characters, and the question is one of comparative likeness only. Systematists may agree that certain characters are more important than other characters, but they would never agree as to what characters are important enough to be regarded as specific in comparison with those which are only racial. In fact, when we come to the point, we find that most systematists do not in practice distinguish species from races on the ground that the former are practically constant, whereas the latter are not, but rather on the ground that they regard the characters which they use to distinguish species as more important than those which they are willing to accept as merely racial.

But what is more important and less important is a question not only of individual opinion at any given time, but it is also a question which depends on the means of analysis at our disposal, and these change from time to time. Surely there never lived a better systematist than Elias Fries, and at the time of

its publication, in 1821-32, his *Systema Mycologicum* was certainly a masterpiece. If the species described by him in genera, such as *Sphæria*, for example, which were then considered valid, are no longer recognized as such, it is not because in limiting his species as he did Fries did not employ with remarkable skill the same scientific principles of classification as the mycologists of to-day, but mainly because the modern application of the microscope to the study of the spores and some other characters has brought out facts unknown at the beginning of the century. The species of Fries have been split up and changed in many respects, and while we feel sure that the modern classification, thanks to improved microscopes, is an improvement on his, who shall dare say that hereafter some present unknown and unsuspected method of analysis may not furnish facts which will overturn our present system?

I should feel that I ought to apologize for bringing up a subject so very, very threadbare, were it not that some botanists shrink from acknowledging the fact that what we botanists call species are really arbitrary and artificial creations to aid us in classifying certain facts which have been accumulated in the course of time, and nothing more. So long as we entertain even a lingering suspicion that they are anything more, systematic botany will not be able to accomplish its real object, which is certainly very important. We are all convinced, theoretically at least, that not only are all plants gradually changing, and sooner or later will no more be what they now appear to us to be than they are now what they were in times past, and we also know that the means which we have of studying them are changing as well. Our so-called species are merely snapshots at the procession of nature as it passes along before us. The picture may be clear or obscure, natural or distorted, according to our skill and care, but in any case it represents but a temporary phase, and in a short time will no longer be a faithful picture of what really lies before us; for we must not forget that the procession is moving constantly onward, and at a more rapid rate than some suspect. Better cameras will be invented, and when another generation of bota-

nists snap off their pictures, they will undoubtedly look back with pity, if not with contempt, on our faded and indistinct productions.

Whether or not species really exist in nature is a question which may be left to philosophy. Our so-called species are only attempts to arrange groups of individual plants according to the best light we have at the moment, knowing that when more is known about them our species will be remodeled. We should not allow ourselves to be deluded by the hope of finding absolute standards, but it should be our object to arrange what is really known, so that it can be easily grasped and utilized. Utility may, perhaps, sound strange, and may seem to some to be a very low aim in science, but in the end utility will carry the day in this case, for systematic botany is a means, not an end. Its true object should be to map out the vegetable kingdom in such a way that all known plants are grouped as clearly and distinctly as possible, in order that the horticulturist, the forester, the physiologist, may be able to obtain the facts needed by them in their work. Our present knowledge may not be sufficient to enable us to draw all the contours sharply, or to lay down accurately all the lines, but our work certainly should not be blurred by subtleties and purely metaphysical refinements. The best systematist is not he who attempts to make his species conform to what he believes to be the ideal of nature, but he who, availing himself of all the information which the histology, embryology, and ecology of the day can furnish, defines his species within broad rather than narrow limits, in clear and sharply cut words which can be readily comprehended and do not force one to resort to original and perhaps single specimens to learn what the author of the species really meant.

The end which we all wish ultimately to reach is a knowledge of how living plants act; but in the process of obtaining this knowledge it is necessary to call to our aid not only the physiologist, but also the systematist and the paleontologist; for there are many questions ultimately to be settled by the physiologist for which the information furnished by the systematist must serve as a basis, and the geological succession must be

supposed to throw some light on present conditions. It is no disparagement to systematic botany to say that it should look towards physiology as its necessary supplement; for, on the other hand, physiology must lean on systematic botany in attempting to solve many of its problems, and the scientific basis of both rests on histology, morphology, in the modern sense, and embryology. The qualifications needed in a physiologist are so different from those required in a systematist that no one is warranted in speaking of one as of a higher grade than the other. If it has become the fashion in some quarters to assign the systematist to a secondary place, it cannot be attributed to the fact that his work is necessarily inferior in quality, but is rather due to the fact that in too many cases systematists have failed to recognize what should be the legitimate aim of their work.

The utilitarian tendency is well shown by what has been said in speaking of bacteria and *Saccharomycetes*. Did time permit, and were the subject not one which would not readily be followed with patience by an audience at this late hour, other instances, especially in *Ustilaginaceæ*, might be given to illustrate further the point in question. The bacteriologist bases his species on grounds which he thinks best suited to enable him to group together intelligently the plants he is studying, and it is nothing to him that others say that his species are not species, but races. After all, the question whether certain forms are to be considered species or races is in many cases merely a question of how much or how little we know about them. The races of one generation of botanists often become the species of the next generation, who, as they study them more minutely and carefully, discover constant marks not previously recognized. As systematic botany develops in the future, it may very well become the study of races rather than species as we now consider them. In some cases, as in the *Uredinaceæ*, the time may be not far distant when this condition of things will be reached. We also feel warranted in believing that hereafter physiological characters will assume even a greater importance than at present in the characterization of species. If there are some among my hearers who do

not agree with me as to the importance to be attached to utility, I think that we shall all agree that in discussing the work of botanists in other departments than our own, it would not be wise to exact a rigid conformity to our individual conceptions of species as distinguished from races.